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Distribution and habitat associations of the critically endangered bird species of São Tomé Island (Gulf of Guinea)

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Summary

São Tomé holds 20 endemic bird species, including the little known and critically endangered dwarf olive ibis *Bostrychia bocagei*, São Tomé fiscal *Lanius newtoni* and São Tomé grosbeak *Neospiza concolor*. We conducted a systematic survey of the core forest area, performing 1680 point counts and compiling occasional observations, which enabled the identification of new areas of occurrence for the target species. Maxent distribution modelling suggested that the ibis and fiscal have roughly half of the potential area of occurrence that had been assumed (127 and 117 km^2, respectively), while more than doubled that of the grosbeak (187 km^2). The southwest central region of the island, most of which is included in the São Tomé Obô Natural Park, has the highest potential for the critically endangered birds. We confirmed the association of all target species with native forest. The ibis preferred high tree density, while the fiscal selected low tree density and intermediate altitudes, contradicting the widespread view that it is a dense lowland forest specialist. Despite very restricted ranges, population sizes seem to be larger than previously assumed. These results suggest that the fiscal and grosbeak might be better classified as endangered, while the ibis should maintain its status under different criteria, due to a very restricted range during the breeding season. This work provides vital ecological knowledge to support conservation action focusing on these species and their habitats. Namely it highlights the need to improve the effectiveness of the São Tomé Obô Natural Park in protecting its unique biodiversity.

Keywords: Dwarf Olive Ibis *Bostrychia bocagei*, São Tomé fiscal *Lanius newtoni*, São Tomé grosbeak *Neospiza concolor*, IUCN Red List, São Tomé and Príncipe

Sumário

São Tomé alberga 20 espécies endémicas de aves, incluindo a galinhola *Bostrychia bocagei*, o picanço *Lanius newtoni* e o anjoló *Neospiza concolor*, todos pouco conhecidos e em perigo crítico. Prospectámos sistematicamente o bloco central de floresta, realizando 1680 pontos de contagem e compilando observações ocasionais, que permitiram identificar novas áreas de ocorrência para as espécies alvo. A modelação de distribuição usando Maxent sugere que a galinhola e o picanço têm aproximadamente metade da área potencial de ocorrência que havia sido assumida (127 e 117 km^2, respectivamente), enquanto que mais que duplicou a do anjoló (187 km^2). A região centro e sudoeste da ilha, maioritariamente incluída no Parque Natural do Obô de São Tomé, tem o potencial mais elevado para as aves criticamente ameaçadas. Confirmámos a associação de todas as espécies alvo com a floresta nativa. A galinhola preferia densidades arbóreas elevadas, enquanto que o picanço seleccionou densidades arbóreas baixas e altitudes intermédias, contradizendo a perspectiva de que se trata de um especialista de floresta densa de baixa altitude. Apesar das distribuições muito restritas, os tamanhos populacionais aparentam ser maiores do que assumido anteriormente. Estes resultados sugerem que o picanço e o anjoló poderão ser melhor classificados como em perigo, enquanto que a galinhola deverá manter o seu estatuto, sob critérios distintos, devido à distribuição muito restrita durante a época reprodutora. Este trabalho fornece conhecimento ecológico vital para acções de conservação focadas nestas espécies e nos seus habitats. Nomeadamente evidencia a necessidade de melhorar a eficácia do Parque Natural do Obô de São Tomé a proteger a sua biodiversidade única.

Palavras-chave: galinhola *Bostrychia bocagei*, picanço *Lanius newtoni*, anjoló *Neospiza concolor*, Lista Vermelha da UICN, Floresta tropical húmida, São Tomé e Príncipe

Introduction

The island of São Tomé (Gulf of Guinea, central Africa) is an important centre of endemism (Jones 1994). The number of endemic birds it holds is particularly remarkable for a small island (Stattersfield *et al.* 1998, Kier *et al.* 2009, Buchanan *et al.* 2011, Le Saout *et al.* 2013). It has 50 resident bird species, of which 17 are single-island endemic species, three are Gulf of Guinea endemic species and eight are endemic subspecies, ranging across eight orders and 19 families (Jones and Tye 2006, Melo and Jones 2008). The island is also unusual among oceanic islands with isolated and unique avifaunas in that there are no recorded anthropogenic extinctions of birds (Jones and Tye 2006).

The endemic avifauna of São Tomé is clearly associated with the persistence of the island's forest dominated landscape (de Lima *et al.* 2013a). Preserving the remaining native forests and restoring degraded habitat are top conservation priorities, namely within and around the São Tomé Obô Natural Park (ONP), where most of the endemic species are found (de Lima 2012, Ndang'ang'a *et al.* 2014). These forests are under high level anthropogenic pressure (Salgueiro and Carvalho 2007). Threats such as land-use intensification, overexploitation and invasive species are likely to continue to have a strong impact on forest ecosystems and on the endemics in the nearby future (Jones *et al.* 1991).

Nine of São Tomé's endemic bird species are currently classified as threatened, including three which are critically endangered; the dwarf olive ibis *Bostrychia bocagei*, the São Tomé fiscal *Lanius newtoni* and the São Tomé grosbeak *Neospiza concolor* (IUCN 2013, Ndang'ang'a *et al.* 2014). The ibis is a lowland species found in old-growth or mature secondary rainforest in the south and centre of the island, and it breeds from September to February (Jones and Tye 2006, Maia *et al.* 2014, Azevedo 2015, Margarido 2015). The fiscal is known only from well-preserved forest, with low understorey density and in areas of high rainfall (Jones and Tye 2006), occurring from the lowlands up to 1395 m above sea level (Maia and Alberto 2009). The grosbeak was thought to be a lowland old-growth forest specialist, but recent observations in secondary forest at 1400 m a.s.l. suggest that it might be more widespread than previously thought (Solé *et al.* 2012).

The implementation of effective conservation measures, requires basic ecological knowledge, which is currently lacking. A better knowledge of distribution and habitat associations is needed in order to identify target areas for intervention and protection, monitor population trends, manage the habitat and tackle threats. Here we describe an intensive survey of this island's core forest ecosystems that, together with *ad hoc* observations, has been used to produce maps of potential species distribution and to identify the areas of the island which are most important for all three species, applying reserve selection algorithms. We also describe broad habitat associations for the species. Finally we assess the implications of this knew information for reviewing the conservation status of the species and to guide conservation activities.

Methods

Study area

São Tomé (857 km^2) is located just north of the Equator, 255 km west of continental Africa and belongs to the small island nation of São Tomé and Príncipe. The island is rugged, especially in the centre and southwest, with several peaks above 1500 m and the highest peak, Pico de São Tomé, at 2024 m. The mountainous topography creates strong climatic gradients, with the annual rainfall ranging from less than 600 mm in the northeast to more than 7000 mm in the southwest, and the mean annual temperatures ranging from around 30º C at sea level to 18º at higher altitudes. Humidity and cloud cover are high throughout the year for most of the island, but there is a well-marked seasonality. The main dry season, locally known as *gravana*, extends from mid May to early September and is characterised by low rainfall and lower temperatures. The rainy season extends through the rest of the year, with a small dry season, the *gravanito*, occurring between December and February (Silva 1958, Tenreiro 1961).

The native forest can be separated in four main types, differentiated by climatic conditions and plant species composition; mangrove, lowland, montane and mist (Monod 1960). The mangrove is restricted to small coastal areas. Lowland forest goes from sea level up to 800 m and is characterised by a sparse understorey, and a high and dense canopy. Montane forest spans 800 to 1400 m a.s.l. and has a high tree density and species richness, with medium understorey and epyphitic density. Mist forest occupies the summit of the island and is typically much shorter, with sparse tree cover and very high epyphitic densities.

The island was first described as being entirely covered by dense tropical forest, but since then, humans have extensively changed its ecosystems (Eyzaguirre 1986). At least 10 % of the island is now covered by non-forested land-use types, such as oil palm monocultures, horticulture and open savanna. The remaining area is covered by similar extents of shade plantation, secondary forest and native forest (Salgueiro and Carvalho 2007). The latter persisting only in mountainous portions of the island, where human presence remains scarce. Most of these best preserved forests are now classified as ONP (DGA 2006). The Park extends through most of the centre and southwest of the island, covering nearly one third of it, but enforcement is weak and protection is not very effective (de Lima *et al.* 2013b).

This study focuses on the three critically endangered bird species endemic to São Tomé; the dwarf olive ibis, the São Tomé fiscal and the São Tomé grosbeak. The ibis is presumed to occupy an area of 213 km^2, with a declining population of 70 to 400 individuals (IUCN 2013). It is a lowland species found in old-growth or mature secondary rainforest in the south of the island. It is usually found feeding on the ground and it breeds from September to February (Jones and Tye 2006, Maia *et al.* 2014, Azevedo 2015, Margarido 2015). It is threatened by habitat loss and degradation, hunting and human disturbance, with climate change and predation by exotic species being considered as potential serious threats (Ndang'ang'a *et al.* 2014).

The fiscal is thought to occupy 260 km^2 and, as a precautionary measure, it is assumed to have a population smaller than 50 adult individuals (IUCN 2013). It is known only from well-preserved forest, with low understorey density and in areas of high rainfall (Jones and Tye 2006). It has been found from the lowlands up to 1395 m a.s.l. (Maia and Alberto 2009, Lewis 2015). It is usually heard in the distance or found perching on low-lying branches, from where it flies to hunt small invertebrates (Jones and Tye 2006, Lewis 2015). There are some indications that it breeds from November to February. Habitat degradation by exotic plant species is considered a potential threat (Ndang'ang'a 2014).

The grosbeak is presumed to occur in an area of 88 km^2 and, as a precautionary measure, it is assumed to have a population smaller than 50 adult individuals (IUCN 2013). Thought to be a lowland old-growth forest specialist, restricted to the South of the island, the species was recently found using an area of secondary forest in the central mountain range, at an altitude of 1400 m a.s.l.. It has also been found feeding on fruits of relatively abundant and widespread species, some of which are typical of disturbed areas. These new observations suggest that the scarcity of records for this species might be linked to its shy behaviour, and that it might be more abundant and widespread than previously thought (Solé *et al.* 2012). The hypothesis is further supported by its high level of genetic diversity (Melo 2006). Habitat degradation due to human disturbance and spread of exotic species have been identified as the major threats to the survival of this species (Ndang'ang'a *et al.* 2014).

Survey design

We gathered occasional and systematic observations of the critically endangered bird species of São Tomé. Occasional observations included our own sporadic records and those collected by other ornithological researchers over the last 15 years. We contacted those authors and compiled all available information in a database with a GIS component, based on locations recorded on GPS.

Systematic surveys of São Tomé's main forest block took place between 2013 and 2015. The study area was divided into 99 square tetrads of 4 km^2 (Fig. 1). We surveyed a randomly selected quarter of each tetrad throughout the study area and more intensively in some areas, such as the southeast (de Lima *et al.* 2013b). In each 1 km^2 quarter we undertook five 10 minute point counts, separated by at least 200 m. When feasible, point counts were scattered across the 1 km^2 quarter so as to represent environmental variability roughly in proportion of its availability, namely in terms of habitat type, altitudinal gradients, and distance to rivers and roads. The number of individuals of each critically endangered bird species detected during each point count was recorded. The location and altitude of each point were registered using a GPS. Habitat at each point was assessed in terms of broad land-use type, slope, number of trees and understorey density (Table 1). To assess seasonality, sampling took place during the main dry season (*gravana*) of 2013 and 2014, and during the *gravanito* of

2014 and 2015, which corresponds to a small dry season at the end of the breeding season for most bird species in São Tomé (Jones and Tye 2006).

[Insert Table 1 and Fig. 1 around here]

Species distribution models

Species distribution models (SDMs) were created using Maxent in the "dismo" R package (Hijmans *et al.* 2015; R Development Core Team 2015). Maxent is a machine learning method that produces niche models from environmental data, and has been found to perform well in comparison to other SDM methods (Elith and Graham 2009).

We created a SDM for the annual, *gravana* (long dry season) and *gravanito* (short dry season) distribution of each species. Given that the exact dates for the seasons can vary, the *gravana* was truncated to June, July and August, and the *gravanito* to January and February. We identified 33 potential predictor variables for inclusion in the SDMs: 19 bioclimate layers (Hijmans and Cameron 2005 - www.worldclim.org/bioclim), 12 normalised difference vegetation index (NDVI) layers (Spot-vegetation sensor through VITO - www.spot-vegetation.com), elevation (Jarvis *et al.* 2008) and slope (created from the elevation layer). The NDVI layers for a thirteen year period (1999-2012) were combined to create a set of monthly averages, and used as a continuous summary of land cover. All predictor variables were standardised to a 1 km^2 spatial scale and processed using ArcMap version 10.2. We created a set of uncorrelated predictor variables and a set of predictor variables that had the greatest average percentage contribution to the maximal model (Table S1). For the seasonal models, only the corresponding NDVI layers were retained.

The SDMs were built using the systematic surveys as training data and tested using the occasional observations (Table S2), except for the grosbeak in the *gravana*. In this case, because there were too few systematic observations, both sets of observations were combined as training data and the resulting model was not tested. We used 886 pseudo-absences in Maxent, the number of non-duplicated training records, unique records for each 1 km^2 raster cell. The optimal feature function combination was identified based on the number of unique sample points (Phillips and Dudík 2008), the "ENMeval" R package (Muscarella *et al*. 2014; R Development Core Team 2015) was used to run a series of models with varying regularisation values (0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5 and 5), and the final model was chosen based on AICc (Warren and Seifert 2011).

The final models were created with a raw output for calculating the model AICc. Ten cross validations were undertaken to generate folds of randomly selected presence data, allowing us to run each model ten times, exclude each fold in turn and use the fold to validate the data (Phillips and Dudík 2008). This enabled us to assess whether the response curves were smooth and biologically sensible. To aid interpretation, these models were repeated with a logistic output, being partitioned using the mean equal training sensitivity and specificity threshold values to identify the minimum area of land required for each species. This threshold was chosen because it minimises the rate of false positives and negatives. We calculated the spatial overlap between the SDM of each species for the predicted annual, *gravana* and *gravanito* distribution, using the "calc.niche.overlap" function of the "ENMeval" R package (Schoener's D and Warren's I statistics – R Development Core Team 2015) and Map Comparison Kit 3.2.3. (Cohen's Kappa statistic – Visser and De Nijs 2006).

Spatial conservation planning

We used the spatial conservation planning software 'Zonation' to identify important areas for the study species, in the three periods considered and giving equal weight to each species. This software produces a hierarchical prioritisation based on the conservation value of sites (Moilanen *et al*. 2005; Moilanen 2007), using a complementarity based algorithm that iteratively removes the cells whose loss causes the smallest decrease in conservation value in the remaining network. The resulting hierarchy of nested outputs correspond to different degrees of conservation value within the landscape and may be used as a guide to determine the level of protection needed. It differs from previous target based planning or maximum coverage approaches that provide a single optimal output (Moilanen 2007). One grid cell was removed in each iteration step (warp factor). The spatial overlap between the three Zonation outputs was calculated using the "calc.niche.overlap" function from the "ENMeval" R package (Schoener's D and Warren's I statistics – R Development Core Team 2015).

Habitat associations

We used generalised linear models (GLMs – Bolker *et al.* 2009, Zuur *et al.* 2009, R Development Core Team 2015) to assess the influence of environmental variables (altitude, slope, number of trees, understorey density, habitat type and season) on the presence of each species. There were 607 point count locations from the *gravanito* and 316 point count locations from the *gravana*, for which we had a complete characterization of all environmental variables. Since there was a high prevalence of absence of critically endangered birds during the point counts, presences were modelled against data from an equal number of randomly selected point counts during which each species had not been recorded. To identify which variables had the greatest support for explaining the presence of the critically endangered birds, we used model averaging and relative variable importance based on second-order Akaike information criterion (AICc) automated model selection (Burnham and Anderson 2002, Barlow *et al*. 2010), from the "MuMIn" R package (Barton 2013, R Development Core Team 2015).

Results

We sampled 720 point counts during the *gravanito* and 960 during the *gravana*. In total we recorded 33,137 birds, belonging to 39 species, including the 20 endemic species and all endemic subspecies, except the harlequin quail *Coturnix delegorguei histrionica* and the barn owl *Tyto alba thomensis*. We detected 38 ibises in 21 point counts, 111 fiscals in 86 point counts and 22 grosbeaks in 16 point counts. The larger sampling effort during the *gravana* was not reflected in records for the critically endangered birds, with just 18 ibises in 8 points, 46 fiscals in 35 points and 3 grosbeaks in 3 points from this season.

Distribution

We obtained records of new areas of occurrence for all three of the target species. The ibis was registered along the Lembá, Ana Chaves and Yo Grande river valleys, and in the proximities of the Maria Fernandes Peak, outside the ONP. The fiscal seems to occur mostly at mid altitudes south of Pico de São Tomé and around the Cabumbé Peak. The distribution of the grosbeak was greatly expanded, with records from Morro de Dentro, Ana Chaves Peak, the Lembá river valley and the southeast slopes of Cabumbé Peak. The presence of the grosbeak in high altitude was confirmed at several locations.

The SDMs scored generally high in the AUC test, ranging from 0.80 ± 0.10 SD to 0.95 ± 0.07 SD (Table S3). The models using all significant predictors always performed better than those using the uncorrelated set of predictors, except for the fiscal in the *gravana*. The variables that best predicted the presence of the three target species for the annual models were those related to: elevation; NDVI, especially in June; and precipitation, namely during the wettest and warmest months (Table S4). The variables related to precipitation were consistently chosen as predictors for the presence of the bird species across the seasons, most notably for the ibis.

The logistic outputs from the SDMs were turned into binary outputs of potentially occupied and unoccupied 1 km^2 square cells, based on the equal training selectivity and specificity thresholds. The resulting maps (Fig. 2a, 2b and 2c) indicated that, across the whole year, the potential area of occurrence was 127 km^2 for the ibis, 117 km^2 for the fiscal and 174 km^2 for the grosbeak. During the *gravana* these areas expand to over 165 km^2 for the ibis, 197 km^2 for the fiscal and 190 km^2 for the grosbeak, while in the *gravanito* they change to 65, 113 and 201 km^2, respectively (Fig. S1). There is a strong spatial overlap in the seasonal distribution of each species, with the ibis exhibiting the most accentuated seasonal changes in distribution (Table 2, Fig. S1).

The southwest central region of São Tomé has high potential for the occurrence of the three critically endangered birds, and was thus identified as the most important area of the island in the output of the zonation analysis (Fig. 2d). This key area for conservation is largely coincident with the ONP, namely 99.1% for the top 10 % threshold, and 82.7 % for the top 25 % threshold.

[Insert Table 2 and Fig. 2 around here]

Habitat associations

We recorded the ibis in 13 point counts with complete habitat characterization, the fiscal in 75 and the grosbeak in 12. Comparing the habitats characteristics of these locations with that of an equal number of unoccupied locations, indicated that the three species showed a preference for native forest. Additionally, the dwarf olive ibis selected areas with higher number of trees and was detected mostly during the *gravanito*, while the fiscal preferred a lower number of trees and intermediate altitudes (Table 3, Fig. 3 and S2).

[Insert Table 3 and Fig. 3 around here]

Discussion

The comprehensive survey of São Tomé forests has allowed, together with information gathered from other researchers, a significant improvement on our knowledge about the distribution, ecology and conservation status of the São Tomé dwarf olive ibis, fiscal and grosbeak.

Distribution

We have greatly increased the number of confirmed locations for all of São Tomé's critically endangered bird species, and gained a better understanding of the distribution of their potential habitat. We have found that the potential distribution of both the ibis and the fiscal are much more restricted than previously assumed, having changed from 213 to 127 km^2 and from 260 to 117 km^2, respectively. The grosbeak, on the other hand, seems to be more widespread, with surveys having extended its potential range from 88 to 187 km^2. The ibis also seems to have strong seasonal changes in distribution, being restricted to just 65 km^2 during its breeding season, in the *gravanito*.

All target species are strongly restricted to the south of the island, and notably to the southwest. The ONP covers most of this area of habitat with high potential for the three species, but not all of it. Namely it does not include 38 km^2 of the top 25% priority areas (Fig. 2d). Bearing in mind that the ONP covers nearly one third of the island and is supporting the conservation of many other biodiversity components, it is still well located for the protection of São Tomé's critically endangered bird species.

Habitat associations and threats

We confirmed that the three target species are strongly linked with the occurrence of native forest. In addition, the ibis is associated with areas with a higher number of trees, and the fiscal with areas with a lower number of trees at intermediate altitudes.

The ibis seems to have a preference for dense forests, in flat areas and with large trees (Margarido 2015), which are the most prone to human impacts, such as hunting, logging and deforestation. However, the species is not restricted to lowland, as we have found it at 950 m a.s.l.. Its habitat preferences in combination with a strong seasonality pose a reason for serious concern, since it concentrates during the breeding season in a very small region, next to over 30 km^2 of recently implemented oil palm monoculture, and to the proposed location for a large hydro-electric dam (de Lima *et al.* 2013b, Azevedo 2015). Of São Tomé's critically endangered bird species, the ibis is also the only one targeted by hunters (Carvalho *et al.* 2015). Recent interviews revealed hundreds of ibises being killed every year, clearly surpassing any previous estimates and making this a key threat to the survival of this species (Sampaio *et al.* 2016).

The fiscal occurs in areas of mid altitude, where the native forest becomes more open. This confirms that this species is not a dense forest specialist (Lewis 2015), which makes sense in light of the habitats used by other shrike species (Yosef 2008). In these specific locations the fiscal can be fairly abundant, but it is hard to estimate population sizes, since large extents of area predicted as suitable for its occurrence are extremely difficult to access (Lewis 2015).

The occurrence of the grosbeak in higher altitude was confirmed in new locations, as was its occasional appearance outside the ONP and in secondary habitats near native forest (Solé *et al.* 2012). These observations suggest that this species might be much more widespread and numerous than previously thought (Jones and Tye 2006). Habitat degradation has been listed as a key threat to its survival (Ndang'ang'a *at al.* 2014), but this might not be as important, since the species is now known to use secondary habitats and to feed on plants typical from degraded areas. Despite the many new records, the grosbeak remains the least seen and most mysterious of São Tomé endemic bird species, which might be due to its discreteness and not necessarily due to its scarceness. This hypothesis is strongly supported by a very significant change in the number of records between season: two birds detected during the *gravana*, against 18 during the *gravanito*. These observations also suggest that the species is most likely breeding during the rainy season. It has been proposed that the grosbeak might hybridise with the very closely related São Tomé seedeater *Serinus rufobrunneus thomensis* (Stervander 2015), and even though this situation requires further investigation, it might pose an additional threat to its conservation.

Finally, we have confirmed the presence of several introduced species (e.g. mona monkey *Cercopithecus mona*, African civet *Civettictis civetta*, black rat *Rattus rattus*, black cobra *Naja melanoleuca* and feral pig *Sus scrofa*) in the vicinities of areas where the critically endangered birds occur. There is no solid evidence that these exotic species are having a negative impact on the birds, and the impact of non native species on São Tomé's native biodiversity remains little studied as a whole (Dutton 1994; Ndang’ang’a *et al.* 2014). Nevertheless, introduced species are well known for having strong negative impacts on island species (Trevino *et al.* 2007), and the precautionary principle advises care until such fears are disproved. Many of these exotic species are likely to predate on birds, others, like many of the invasive plants or the feral pig, might degrade the overall quality of habitat. The quinine plant *Cinchona ledgeriana*, for instance, might pose a serious threat to the fiscal, since it occupies the understorey (Diniz *et al.* 2002), which this bird needs to be open for hunting (Jones and Tye 2006, Lewis 2015).

IUCN Red List conservation statuses

The revised potential distributions presented here could warrant a change in the status of these species in the IUCN Red List (IUCN 2013). The ibis is classified as critically endangered due to having a declining population, smaller than 250 mature individuals and confined to a single location (criterion C2a(ii) – IUCN 2001, IUCN 2013). According to our findings it is unlikely that its population is that small and that this criterion can still be applied. However, the species is restricted to less than 100 km^2 during the breeding season and to a single location, with an inferred continuing decline in the area, extent and quality of its habitat, and in the number of mature individuals, for which we suggest that it should retain its status, under different criteria (B1a,b(iii,v)).

The fiscal and the grosbeak are both classified as critically endangered due to having extremely small population sizes, with less than 50 mature individuals (criterion D – IUCN 2001, IUCN 2013). Our observations, together with those of other authors (Solé *et al.* 2012, Ndang'ang'a *et al.* 2014, Azevedo 2015, Lewis 2015), suggest that their populations sizes are much higher, and that therefore their conservation statuses should be reassessed. We propose that the category of endangered is perhaps more adequate, due to their extents of occurrence being smaller than 5,000 km^2 and being restricted to a single location, with an inferred continuing decline in the number of mature individuals and in the area, extent and quality of their habitats (criterion B1a,b(iii,v)).

Priorities for future research

Most of the areas where the native forest persists are difficult to access due to the very rugged terrain and to a very high annual rainfall. These natural conditions have guaranteed protection from human interference, but have also made it difficult to study their ecosystems and species. This study is part of the most intensive systematic biological survey of these remote areas, during which data on other taxa (e.g. terrestrial vertebrates, land snail and plants) was also collected, allowing improving knowledge on their distribution, ecology and conservation status (e.g. de Lima *et al.* 2016). These surveys have collected extensive evidence on the importance of the native forest for maintaining many of the island's endemic species, but have also shown that each species relies on specific areas of the forest for its survival. For instance, while the ibis is associated with high tree density in the lowlands, the fiscal seems to prefer lower tree densities at intermediate altitudes. These specific habitat associations pose a challenge to conservation prioritization and intervention, as they demand a differential treatment of ecosystems to ensure the persistence of multiple biodiversity components. It is therefore crucial to keep improving our understanding of the relationship between species and ecosystems.

All target species were found more often during the *gravanito*. This suggests that they become more abundant or easier to detect during this season, and further supports the hypothesis that this is their main breeding season, as it has been described for most bird species in São Tomé (Jones and Tye 2006, Maia *et al.* 2014, Azevedo 2015, Margarido 2015). This finding indicates also that this is most likely the best time of the year to monitor these species.

A key priority for further research is to gain more knowledge of potential threats resulting from human activities, such as the collection of forest products (e.g. timber, charcoal, quarry species, palm wine, medicinal plants), and from the intrusion of introduced animal and plant species in native forest (de Lima *et al.* 2013a), as these are also likely to have a distinct impact on each species and ecosystem. The hunting of the dwarf olive ibis is a top priority, as it seems to be posing an immediate threat to the survival of this species. Furthermore, halting it requires a good understanding of complex socio-economic drivers (Carvalho *et al.* 2015, Sampaio *et al.* 2016). This is essential when considering the species restricted breeding range, alongside the fact that hunting pressure may already be limiting the population density in the areas of suitable habitat we have identified.

Implications for conservation

We confirmed that all of São Tomé critically endangered bird species have a very limited distribution, strongly associated with the occurrence of the best preserved patches of native forest. These are mostly located in the centre and southwest of the island and within the ONP (Salgueiro and Carvalho 2007), which despite its legal recognition is weakly enforced (de Lima *et al.* 2013b). Increasing the effectiveness of the park is key to ensure the long-term survival of São Tomé's most threatened avifauna and native forest ecosystems. Nevertheless, it requires significant investment, given the current staff and logistical limitations of the protected area authority. If São Tomé's tropical forest ecosystems and globally threatened biodiversity are to be protected, particular attention needs to be focused on developing and implementing a rigorous enforcement and surveillance programme, which in turn depends on the identification and development of a sustainable financing approach.

Our work has also shown that even the most threatened species might occur outside the ONP boundaries and use secondary forests. These results are a sign of hope for the future of these species, but should be taken with caution since they represent an improvement on the knowledge about their situation rather than a change in their conservation status. It would be important to better understand the conditions in which they use these areas, in order to expand suitable habitat, namely through habitat management, control of human activities and expanding the existing network of protected areas in the island. Much of these secondary habitats fall within a proposed buffer zone, which is under threat from large-scale commodity development, while awaiting for legal recognition (de Lima *et al.* 2013b). Improving the protection of key ecosystems outside the only existing protected area and developing an effective management framework for a more sustainable use of resources in edge forest ecosystems is also critical to protect São Tomé's unique biodiversity.

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Conflict of Interest

None.

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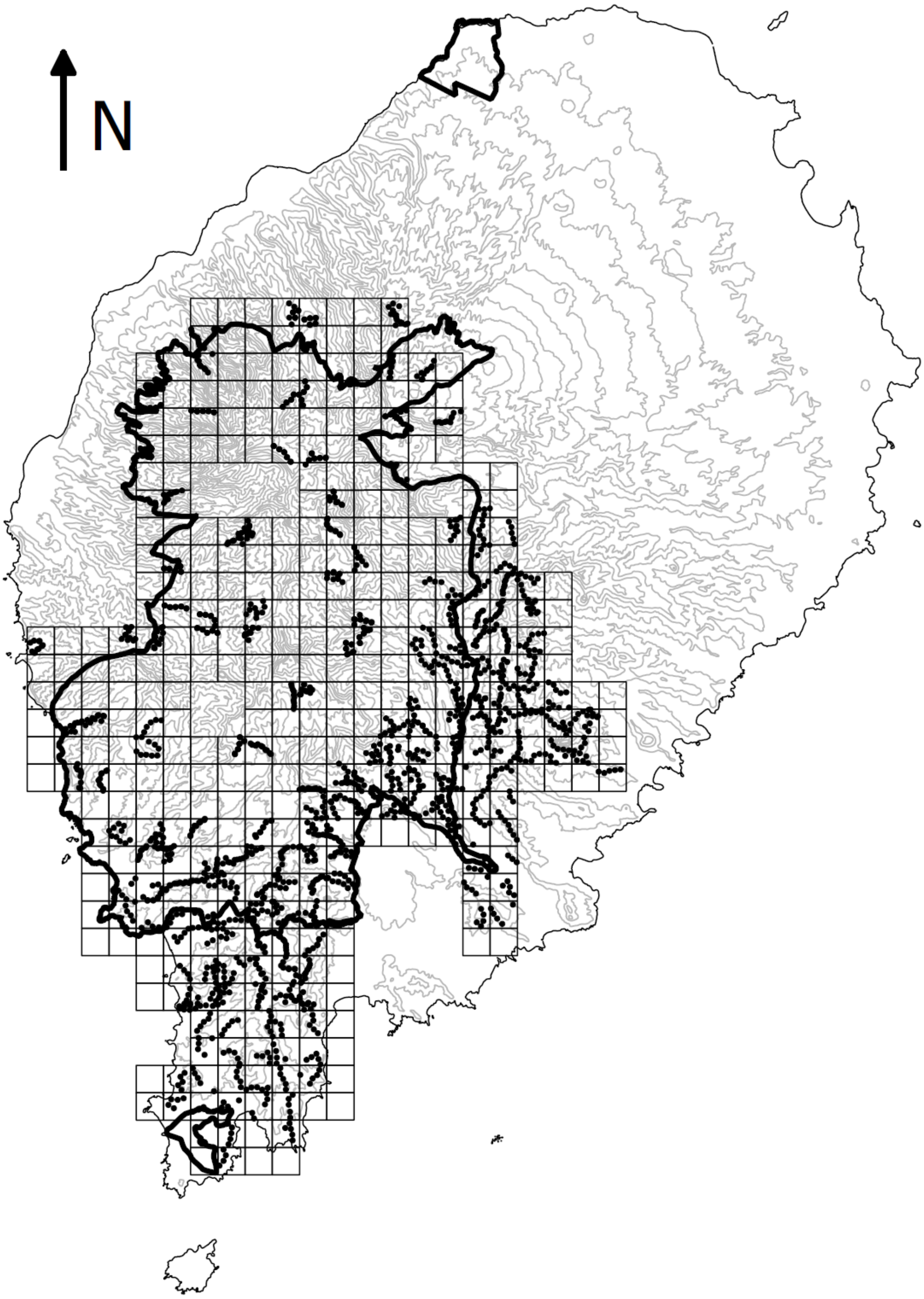
Figure Legends

Figure 1 – Map of São Tomé Island showing study area. The squares represent 1 km^2 quadrats in the 4 km^2 tetrads that were sampled at least once. The dots indicate systematic point counts. The boundaries of the São Tomé Obô Natural Park are shown by the bold black lines. The 100 m contour lines are shown in grey and island outline in black.

Figure 2 – The distribution of São Tomé Dwarf Olive Ibis (a), Fiscal (b) and Grosbeak (c). The black quadrats represent confirmed locations, while the overimposed grey areas represent suitable ranges, according to the categorical annual distribution predicted by logistic MaxEnt modelling. Zonation based on categorical SDM (d) is also shown, with the darkest colours indicating the most important conservation areas and the coolest colours indicate the least important conservation areas (0-19% = almost white, 20-49% = very light grey, 50-74% = light grey, 75-89% = intermediate grey, 90-94% = dark grey, 95-97% = very dark grey and 98-100% = black).

Figure 3 – Relationship between the presence of São Tomé critically endangered bird species and environmental variables. Only the variables with the highest relative importance values for each species are plotted (Table 3).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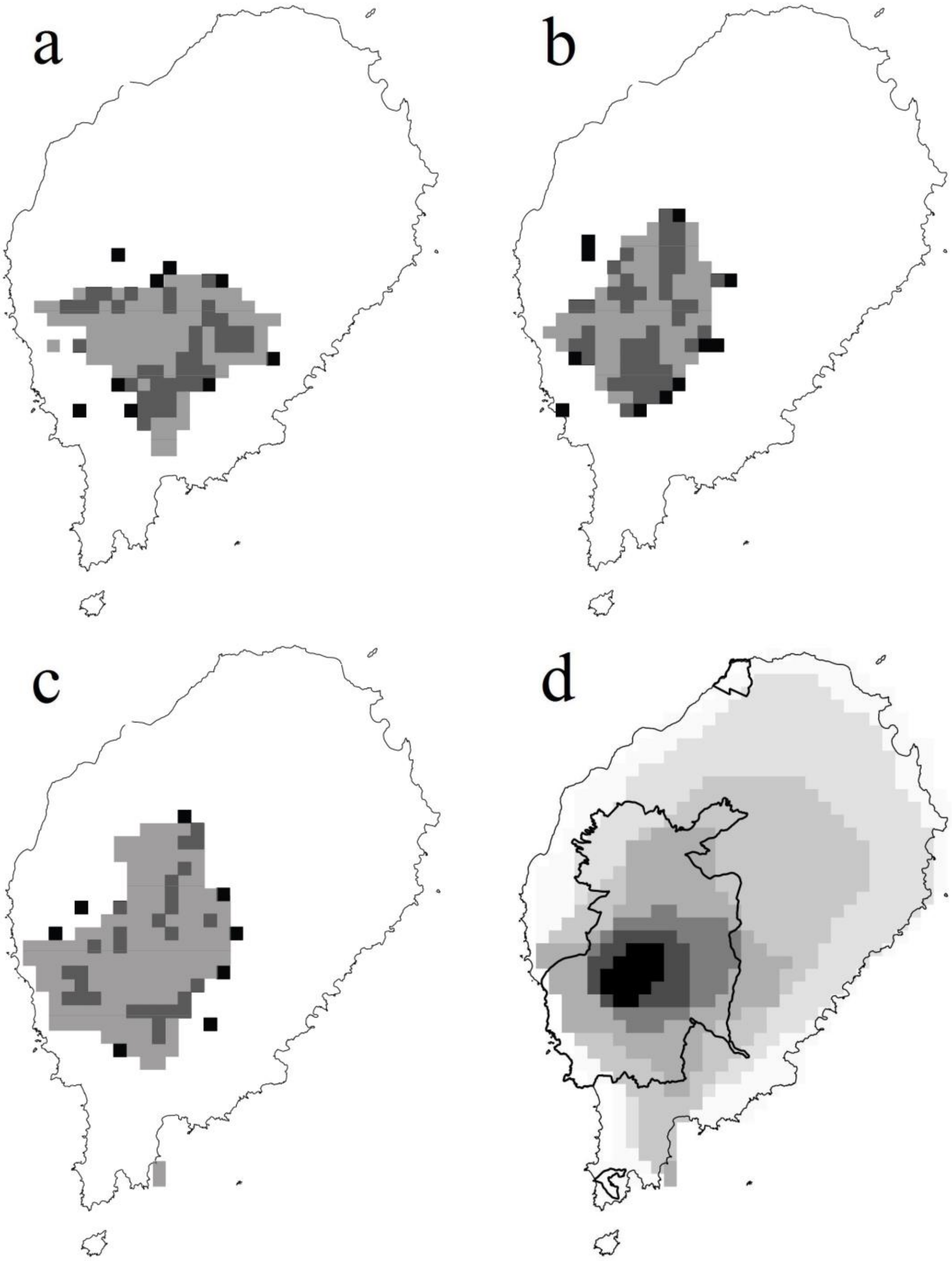
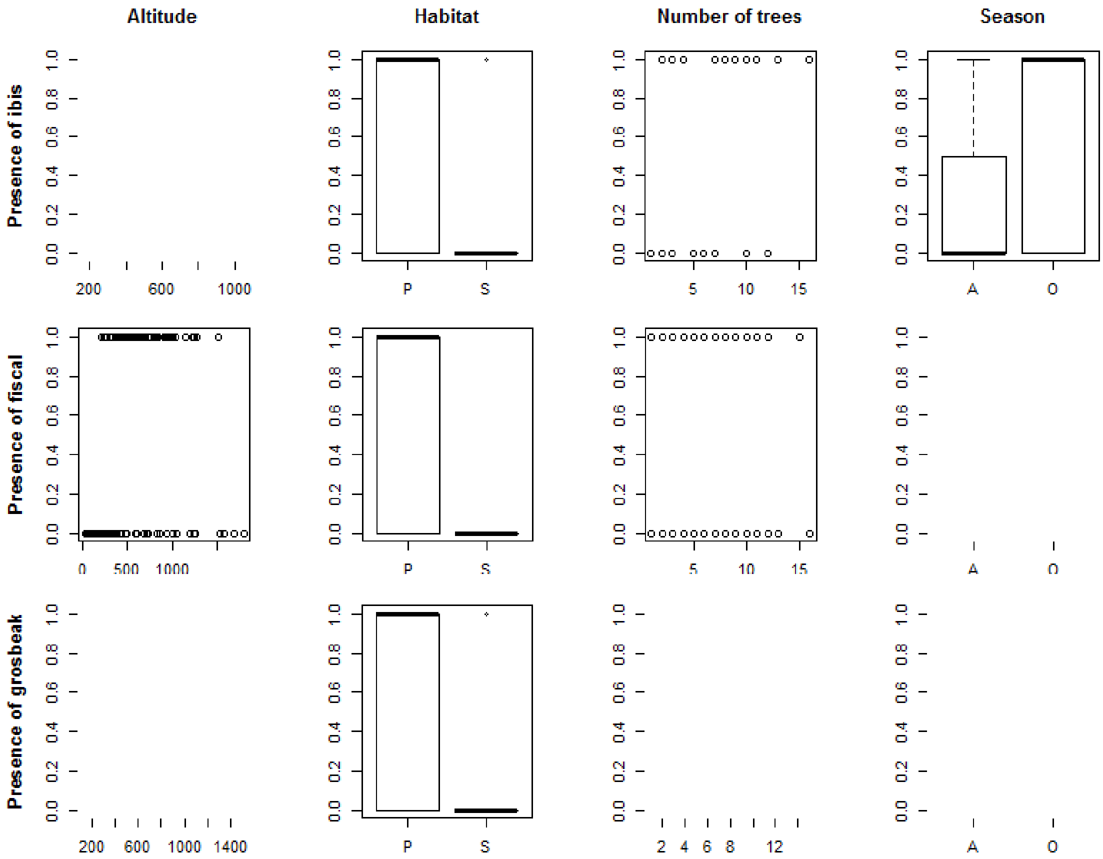


a
b
c
d


Altitude
Habitat
Number of trees
Season
Presence of ibis
Presence of fiscal
Presence of grosbeak
0.0
0.2
0.4
0.6
0.8
1.0
200
600
1000
0
500
1000
200
600
1000
1400
P
S
5
10
15
2
4
6
8
12
A
O

Tables

Table 1 – Habitat characteristics assessed in the 20 m surrounding each point count location.

Characteristic	Description
Habitat type	Native forest, secondary forest or plantation
Slope	1 – none or very soft; 2 – soft; 3 – medium; 4 – steep; 5 – very steep
Number of trees	Count of all trees with diameter at breast height larger than 30 cm
Understorey density	1 – none or very sparse; 2 – sparse; 3 – medium; 4 – dense; 5 – very dense

Table 2. Spatial overlap between categorical Maxent SDM outputs for each and across the three critically endangered bird species. Values correspond to Schoener's D, Warren's I and Cohen's K statistics, respectively. For across the species, only D and I statistics values are shown**.** For D and I statistics, 0 means no overlap and 1 complete overlap. For K 0 means no agreement, values between 0 and 0.20 slight agreement, between 0.21 and 0.40 fair agreement, between 0.41 and 0.60 moderate agreement, between 0.61 and 0.80 substantial agreement and between 0.81 and 1 almost perfect agreement.

Species	**Annual/*Gravana***	**Annual/*Gravanito***	***Gravana*/*Gravanito***
Ibis	0.54/0.61/0.91	0.48/0.67/0.95	0.22/0.35/0.89
Fiscal	0.48/0.62/0.90	0.72/0.73/0.95	0.44/0.58/0.89
Grosbeak	0.47/0.49/0.85	0.53/0.56/0.87	0.66/0.68/0.90
All species	0.84/0.96	0.91/0.98	0.87/0.97

Table 3. Relative importance of variables and averaged coefficients obtained from generalised linear models on the presence São Tomé critically endangered bird species. The grey shading highlights variables with the highest relative importance values (larger than 0.3) and the asterisks indicate variables that on their own perform better than the null model. A relative importance value of 1 means that the variable is included in all best models (Fig. S2). Habitat and Season are factorial variables with positive values corresponding to a preference for secondary forest and *gravanito*, respectively.

	Ibis		**Fiscal**		**Grosbeak**	
	Imp.	**Coef.**	**Imp.**	**Coef.**	**Imp.**	**Coef.**
Altitude	0.236	0.001	0.322*	-0.001	0.207	0.000
Habitat	0.430*	-1.770	1.000*	-20.668	0.650*	-2.171
Number of trees	0.435*	0.197	0.372	-0.071	0.269	-0.128
Slope	0.287	-0.330	0.260	-0.030	0.204	0.072
Understorey Density	0.238	0.292	0.260	0.008	0.242	-0.273
Season	0.412	1.399	0.297	-0.297	0.227	0.633

Supplementary Material

Table S1. Details of predictor variables used to build the SDMs in Maxent.

Name of raster	Description
Bio 1	Annual mean temperature
Bio 2	Mean diurnal range
Bio 3	Isothermality
Bio 4	Temperature seasonality
Bio 5	Maximum temperature warmest month
Bio 6	Minimum temperature coldest month
Bio 7	Temperature annual range
Bio 8	Mean temperature wettest quarter
Bio 9	Mean temperature driest quarter
Bio 10	Mean temperature warmest quarter
Bio 11	Mean temperature coldest quarter
Bio 12	Annual precipitation
Bio 13	Precipitation wettest month
Bio 14	Precipitation driest month
Bio 15	Precipitation seasonality
Bio 16	Precipitation wettest quarter
Bio 17	Precipitation driest quarter
Bio 18	Precipitation warmest quarter
Bio 19	Precipitation coldest quarter
NDVI January	NDVI of named month
NDVI February	NDVI of named month
NDVI March	NDVI of named month
NDVI April	NDVI of named month
NDVI May	NDVI of named month
NDVI June	NDVI of named month
NDVI July	NDVI of named month
NDVI August	NDVI of named month
NDVI September	NDVI of named month
NDVI October	NDVI of named month
NDVI November	NDVI of named month
NDVI December	NDVI of named month
Elevation	
Slope	

- Yearly set ‘A’ of uncorrelated predictor variables: isothermality, temperature seasonality, temperature annual range, precipitation in the driest quarter and January NDVI.
- *Gravana* set of ‘A’ uncorrelated predictors were the same but January NDVI was substituted for July NDVI.
- *Gravanito* set of ‘A’ uncorrelated predictors were the same as the yearly set.
- For the *gravana* set of maximal predictors, only June NDVI, July NDVI and August NDVI were retained.

- For the *gravanito* set of maximal predictors, only January NDVI and February NDVI were retained.

Table S2. Presence data used to build the SDMs in Maxent.

Species	**Season**	**Total number of records**	**Number of unique training records**	**Number of test records**
Ibis	Annual	363	42	82
Ibis	*Gravana*	60	17	19
Ibis	*Gravanito*	77	18	9
Fiscal	Annual	269	39	126
Fiscal	*Gravana*	73	12	49
Fiscal	*Gravanito*	89	18	30
Grosbeak	Annual	74	24	33
Grosbeak	*Gravana*	13	12	0
Grosbeak	*Gravanito*	33	10	13

Table S3. Summary of Maxent model outputs. The grey shading indicates the best models based on AICc and AUC

Spe cies	Peri od	Number of unique training points	Regularization parameters	Predictors	AIC c	AU	Smo oth cur
Ibis	Ann	42	2	All significant	111	0.90	Yes
Ibis	Ann	42	1	A	117	0.86	Yes
Fisc	Ann	39	1	All significant	105	0.90	Yes
Fisc	Ann	39	0.5	A	111	0.88	Yes
Gro	Ann	24	3.5	All significant	323.	0.84	Yes
Gro	Ann	24	4	A	352.	0.76	Yes
Ibis	*Gra*	17	1	All significant	315.	0.85	Yes
Ibis	*Gra*	17	1	A	354.	0.85	Yes
Fisc	*Gra*	12	0.5	All significant	259.	0.81	Yes
Fisc	*Gra*	12	1	A	230.	0.83	Yes
Gro	*Gra*	12	1	All significant	157.	0.87	Yes
Gro	*Gra*	12	1	A	167.	0.84	Yes
Ibis	*Gra*	18	1	All significant	396.	0.94	Yes
Ibis	*Gra*	18	0.5	A	409.	0.94	Yes
Fisc	*Gra*	18	1	All significant	480.	0.91	Yes
Fisc	*Gra*	18	1	A	501.	0.90	Yes
Gro	*Gra*	10	0.5	All significant	152.	0.80	Yes
		10	0.5			0.78 7	

Table S4. Details of predictor variables used in final SDMs for each species and season complement.

Species	Season	Significant variables
Ibis	Annual	Temperature annual range, Annual precipitation, Precipitation driest month, Precipitation seasonality, Precipitation wettest quarter, Precipitation warmest quarter, June NDVI, November NDVI, elevation
Ibis	*Gravana*	Annual precipitation, Precipitation wettest month, Precipitation wettest quarter, Precipitation warmest quarter
Ibis	*Gravanito*	Precipitation wettest month, Precipitation driest month, Precipitation seasonality, Precipitation wettest quarter, Temperature annual range, January NDVI, elevation
Fiscal	Annual	Mean diurnal range, Precipitation wettest month, Precipitation wettest quarter, Precipitation warmest quarter, January NDVI, June NDVI, elevation, slope
Fiscal	*Gravana*	Precipitation wettest month, June NDVI
Fiscal	*Gravanito*	Mean diurnal range, Annual precipitation, Precipitation wettest month, Precipitation warmest quarter, January NDVI, slope
Grosbeak	Annual	Precipitation wettest month, Precipitation wettest quarter, Precipitation warmest quarter, June NDVI, November NDVI, December NDVI, elevation
Grosbeak	*Gravana*	Temperature annual range, Precipitation wettest month
Grosbeak	*Gravanito*	Annual precipitation, Precipitation warmest quarter

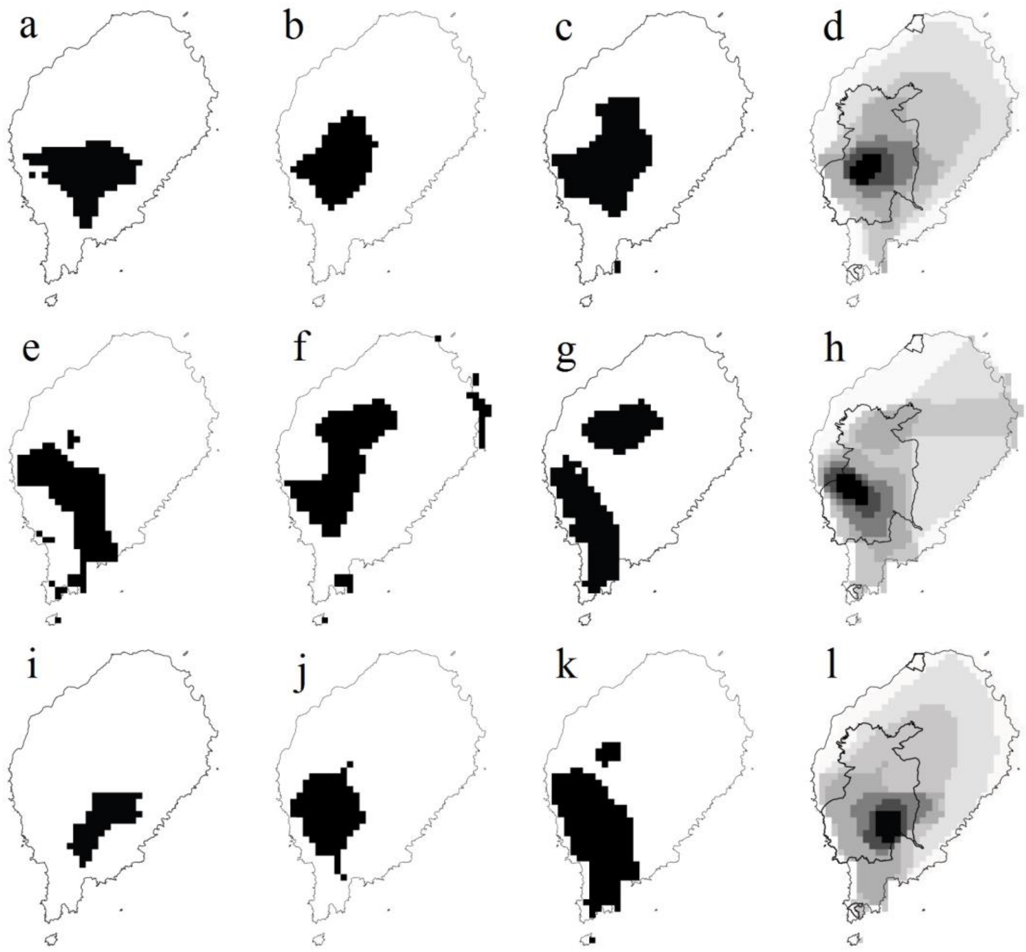
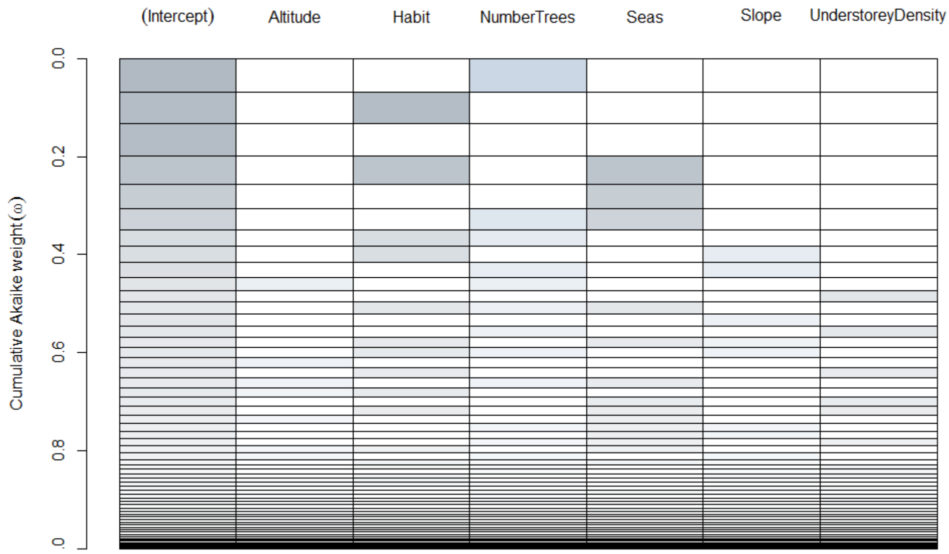
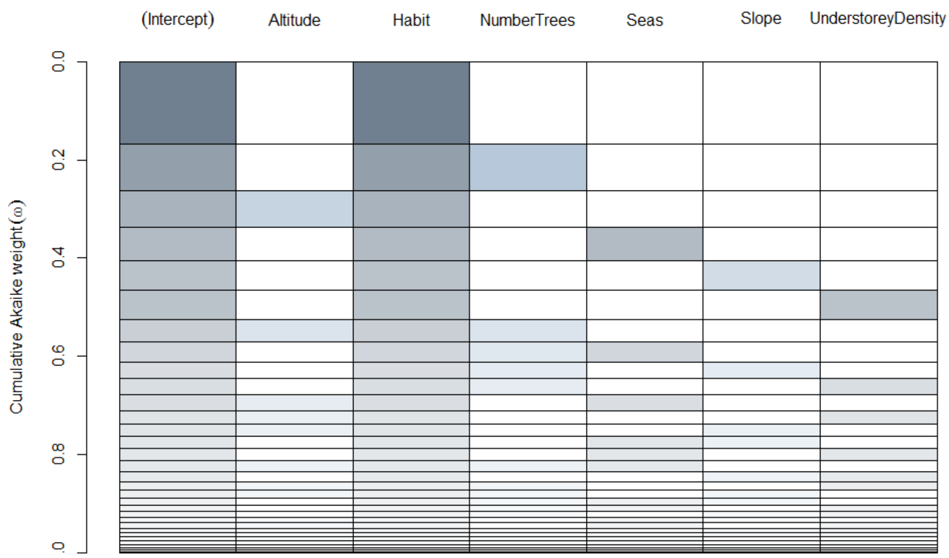


Figure S1 – The categorical distribution model for the São Tomé Dwarf Olive Ibis (a,e,i), Fiscal (b,f,j) and Grosbeak (c,g,k), as predicted by logistic MaxEnt modelling. Quadrats in black are suitable, while those unsuitable are blank. Annual (a,b,c), *gravana* (e,f,g) and *gravanito* (i,j,k) distributions are shown, as well as the corresponding zonation based on categorical SDM (d,h,l). In the zonation panels, the darkest colours indicate the most important conservation areas (0-19% = almost white, 20-49% = very light grey, 50-74% = light grey, 75-89% = intermediate grey, 90-94% = dark grey, 95-97% = very dark grey and 98-100% = black) and the additional black lines shows the boundaries of the São Tomé Obô Natural Park.

(a)


(Intercept)
Altitude
Habit
NumberTrees
Seas
Slope
UnderstoreyDensity
Cumulative Akaike weight (ω)
0.0
0.2
0.4
0.6
0.8

(b)


(Intercept)
Altitude
Habit
NumberTrees
Seas
Slope
UnderstoreyDensity
Cumulative Akaike weight (ω)
0.0
0.2
0.4
0.6
0.8

(c)

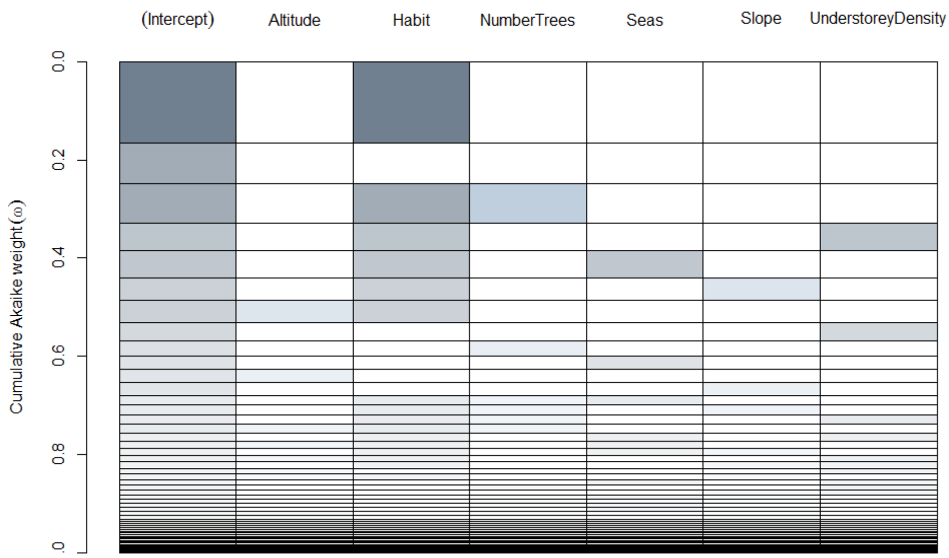

(Intercept)
Altitude
Habit
NumberTrees
Seas
Slope
UnderstoreyDensity
Cumulative Akaike weight (ω)
0.0
0.2
0.4
0.6
0.8

Figure S2 – Results of the automated model selection based on second-order Akaike Information Criterion for the (a) ibis, (b) fiscal and (c) grosbeak. Each line corresponds to a possible model, ranked by the cumulative Akaike weight, and each column to an environmental variable (altitude, habitat type, number of trees, season, slope and understorey density). The colouring of a cell indicates if a variable is present in a model. The taller the cell, the larger the cumulative Akaike weight for the corresponding model.